Field to a forest: Patterns of forest recovery following shifting cultivation in the Eastern Himalaya

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ABSTRACT

The patterns of vegetation recovery in shifting cultivation landscapes that undergo a cycle of clearing, cultivation and forest regeneration are not well understood in Asian tropical forests. We determined forest recovery patterns by comparing species composition, richness and forest structure in early and late fallows formed following shifting cultivation and in an uncut forest site in a mid-elevation subtropical forest in the Indian Eastern Himalaya. We also examined changes in functional traits of tree species to understand recovery processes with succession. Tree species richness in the 12, 25 and 50-year old sites was 37%, 54% and 82% the value of the richness in uncut forest, respectively, while basal area was 33%, 25% and 41% of the value in uncut forest, respectively. Species composition recovery, however, was low; with even the oldest fallow (50-year fallow) being less than 50% similar to uncut forest in terms of composition. Successional sites that recover over long periods may differ compositionally from uncut forest within a shifting cultivation landscape as these forests are often prone to other anthropogenic disturbances. Functional trait analysis revealed that early fallows were colonized by tree species that are animal-dispersed, insect-pollinated with small fruits and seeds, whereas uncut forest and late successional forests were dominated by species that were tall, self-dispersed, wind-pollinated and of high wood density that are dominant mature forest species in the Himalaya. These results are in contrast with the patterns in functional traits of tree species in successional sites from the Neotropics. This points to the importance of site-specificity in succession following shifting cultivation.

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1. Introduction

Shifting cultivation is an agricultural system in which parcels of land are cleared of forests and cultivated for a short period and subsequently left to regenerate for a longer period (Conklin, 1961). Globally, over 300 million people practice shifting cultivation over more than 400 million hectares (Andriesse and Schelhaas, 1987; Kleinman et al., 1996; Mertz et al., 2009). The practice is diverse, ranging from a traditional form that has persisted over several centuries with relatively long fallow periods undertaken in sites adjoining uncut forests to a non-traditional form practiced for economic necessity more recently as a supplementary activity close to urban fringes (Conklin, 1957; Spencer, 1966; Ramakrishnan, 1992). The traditional practice is usually undertaken for subsistence at relatively smaller scales in

comparison with other landuses such as monoculture plantations, pastures, large-scale permanent agriculture (Fox et al., 2000; Seidenberg et al., 2003). Unlike other permanent landuses, for the practice to continue over long periods, communities need to retain secondary and primary forests in the landscape (Delang and Li, 2013).

Since the practice involves a continuous cycle of clear-felling and regeneration, shifting cultivation sites provide an opportunity to understand secondary succession patterns. Shifting cultivation fallows have been shown to recover faster in terms of forest structure and species than other abandoned agricultural lands such as pastures, agroforestry, and monoculture plantations (Ferguson et al., 2001). Although fallows may not completely revert to the original forests if the disturbance is terminated, several parameters have been shown to recover to comparable levels, although over relatively long periods (Guariguata and Ostertag, 2001; Peña-Claros, 2003; Finegan and Nasi, 2004; Delang and Li, 2013). Basal area of trees has been shown to increase over time and reach half the value in the adjoining mature forest within roughly

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three decades in shifting cultivation sites adjoining dry forests (Kennard, 2002; Ruiz et al., 2005) as well as semi-deciduous forests (Kammesheidt, 1999; Toledo and Salick, 2006). Tree density has been shown to initially increase with a decrease or stabilization at later stages of succession (Kammesheidt, 1999; Lebrija-Trejos et al., 2010; Van Do et al., 2010; Aweto, 2013). Plant species richness has been reported to recover to values comparable with those in mature forest in 20–40 years; however, full recovery of species composition, particularly of rare species and species endemic to the region has been reported to take longer than 100 years (Saldarriaga et al., 1988; Vankat and Snyder, 1991; Finegan, 1996; Van Gemerden et al., 2003). Contrasting this, in an Afrotropical site where traditional agriculture was embedded within forests and was undertaken with fallow periods of five to 15 years without the use of fire in creating new fields, species composition in comparison with adjoining forest recovered within 30 years (N'Dja et al., 2008). It is likely that forest recovery is faster in traditional shifting cultivation landscapes than in sites with more recent versions of the practice as shown by some studies (N'Dja et al., 2008). The rate of forest recovery following cultivation is also affected by the number of cultivation cycles in a site (Lawrence et al., 2005).

In addition to documenting forest structure and species diversity in successional sites to understand recovery patterns, an analysis of species functional traits can provide a framework to understand plant ecological strategies and thereby lead to further insights into recovery processes (Verheyen et al., 2003; Poorter, 2007; Raevel et al., 2012). The existing information on functional traits of plants in different successional stages is mostly from the temperate and Neotropical regions (Prach et al., 1997; Tabarelli and Peres, 2002; Verheyen et al., 2003; Flinn and Vellend, 2005; Dölle et al., 2008) and information from Old World sites is largely lacking (but see Asanok et al., 2013; Böhnke et al., 2012, 2014). For instance, while wood density has been shown to be lower in secondary forests in comparison with the values in mature forest in both the regions (Suzuki, 1999; Woodcock, 2000; Asanok et al., 2013), information regarding other functional traits is largely lacking from Old World sites. Among tree species in the Neotropics, the occurrence of wind dispersal decreased, vertebrate dispersal increased, and seed weight and size increased during the successional transition from pioneer to forest stage (Tabarelli and Peres, 2002; Chazdon et al., 2003; Dölle et al., 2008). Prach et al. (1997) found no significant difference between pollination modes of species from early and old successional sites while Chazdon et al. (2003) found that insect pollination was higher and mammal pollination was lower in early successional sites than in old-growth and logged forests.

To compare these trends and to understand forest recovery patterns and processes, we collected information on species richness and abundance, forest structure and functional traits of tree species in different-aged successional sites ranging from 2 to 50 years since cultivation in a traditional shifting cultivation landscape in a subtropical forest in the Eastern Himalaya. We focused on traits that we expected to vary during succession: dispersal mode, pollination mode, seed and fruit size, tree height and wood density. Based on past studies, apriori we had expected tree species in early successional sites to be small-seeded abiotically dispersed species of low wood density in comparison with older successional sites and uncut forest that we expected would be comprised of large-seeded vertebrate-dispersed species of high wood density. We also enumerated species composition of seedlings and saplings to investigate if the species composition patterns and functional traits of the regeneration niche in different successional sites reflected those of the adult tree niche.

2. Methods

2.1. Study area

The study was undertaken in a shifting cultivation landscape around Bomdo village in the Upper Siang district of the state of Arunachal Pradesh in north-east India located at 28.753° N and 94.896° E (Fig. 1). The community forest around the village is contiguous with the Mouling National Park (483 km^2), which is part of the Dihang Dibang Biosphere Reserve (5100 km^2). The average annual rainfall in the district was about 4300 mm (average for years 2010–2013, IMD, 2015). The region has tropical wet- and semi-evergreen forests and sub-tropical broad-leaved forest in the higher areas above 800 m (Singh et al., 1996). The shifting cultivation practice of the *Adi* community in Central Arunachal Pradesh is relatively more systematic in comparison with practices in most of north-east India (Borang, 1997; Teegalapalli and Datta, in press); rather than families cultivating individual plots, 4–8 families in each village cultivate within a single large patch of about 2–4 ha (Teegalapalli and Datta, in press). The fallow cycle; the period within which a cultivated plot is re-cultivated, is 10–12 years which is higher than that practised by several other communities in the region (Deb et al., 2013; Behera et al., 2015). We used a Space-for-Time substitution framework with the assumption that spatial and temporal variation in different-aged successional sites are equivalent (Pickett, 1989). The other assumption was that sites had undergone same number of cultivation cycles since land under cultivation is rotated biennially in the hill slopes around the village (Teegalapalli and Datta, in press).

2.1.1. Vegetation sampling

Different-aged sites or fallows (2, 12, 25, 50 years with two replicates each) following shifting cultivation were selected based on detailed cultivation history maintained by the villagers. The sites were located within 1000 m distance of each other, ranged in elevation from 750 to 1100 m (Fig. 1) and were about 2 ha in area (range: 1.12–3.1 ha, mean [± SE]: 2.23 [± 0.37]), and one of the 50-year old sites was contiguous with uncut forest. Uncut forest in this study represents moderately disturbed uncut forest rather than mature forest that is devoid of any human disturbance.

Vegetation surveys were undertaken between October 2013 and May 2014 in each these sites and in two uncut forest sites adjoining these sites. Trees (diameter at breast height, DBH ⩾ 3 cm) were inventoried and identified to species or genus level in twelve 7 m radius plots located 25 m from each other on alternating sides of a 250-m transect, covering 0.185 ha per site. Overall, we sampled 0.37 ha in each successional stage and each uncut forest site, and a total area of 1.85 ha. The uncut community forest around the village is substantially larger than the successional sites and is contiguous with the forests of the Mouling National Park, therefore in addition to the 24 plots sampled in two uncut forest sites, we sampled 12 more 7-m radius plots, with a total area of 0.55 ha sampled in uncut forest. We enumerated the regeneration comprising of seedlings (height ⩽25 cm) and saplings (height >25 cm to ⩽100 cm) of tree species in each of the four successional stages and the uncut forest sites in 1-m and 3-m radius plots, respectively nested within the 7-m radius plots, respectively. The seedlings and saplings were identified to the species or genus level.

2.1.2. Functional traits

Five functional traits (fruit size, seed size, seed dispersal mode, pollination mode and tree height) of a subset of the data from the entire species pool (70 species of adult trees and 40 species of
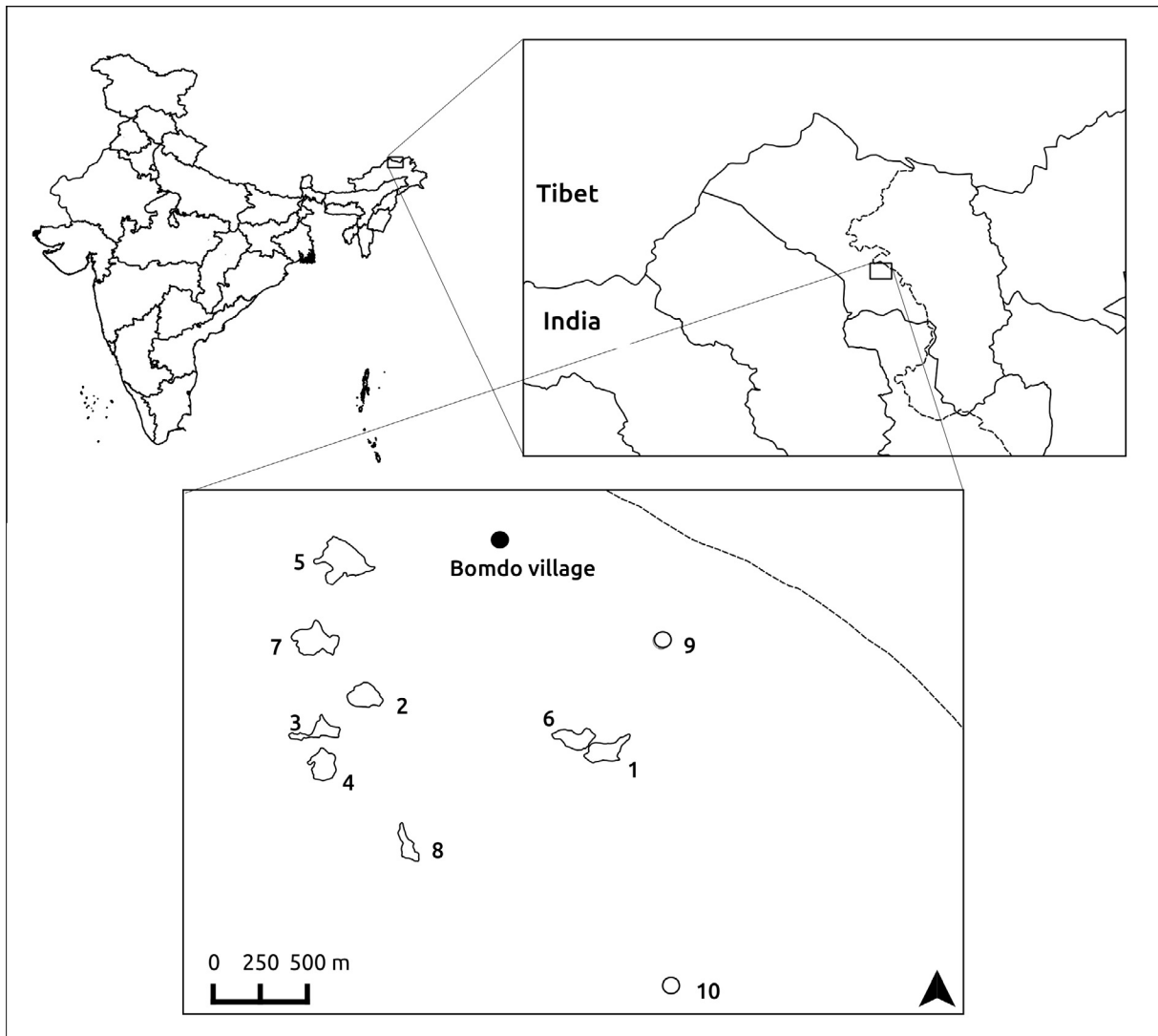
Fig. 1. Study area indicating the location of Siang river (dotted line), Bomdo village and adjoining successional sites (1 and 2 represent the 2-year old successional sites, 3 and 4 represent the 12-year old sites, 5 and 6 represent the 25-year old sites, 7 and 8 represent the 50-year old sites and 9 and 10 represent uncut forest sites). The polygons were mapped by walking around the successional sites with a Global Positioning System unit. Inset map shows the location of the study area in India in the State of Arunachal Pradesh.

seedlings and saplings) were recorded based on both direct field observations and secondary information from floras of the region (Kanjilal et al., 1934; Balakrishnan, 1983; Haridasan and Rao, 1987; Endress, 1994) and published literature (see supplementary information). Wood cores from 46 tree species (3 individuals per species) were collected using an increment borer and dried in an oven for 72 h to estimate wood density (Cornelissen et al., 2003; Chave, 2005; Pérez-Harguindeguy et al., 2013). Density was estimated using the ratio of dry weight to the volume of the core, estimated using the water-displacement method. Wood density data for 24 more species was obtained from secondary information (Reyes et al., 1992; Brown, 1997; Zanne et al., 2009). Of these, information at the genus level (averaged across species reported only from Asia) was used for 18 species for which species level data was unavailable as wood density is a trait that has been shown to be taxonomically conserved at the genus level (Baker et al., 2004; Slik, 2006).

We used floras from the region (Kanjilal et al., 1934; Balakrishnan, 1983; Haridasan and Rao, 1987) and published articles (Datta and Rawat, 2008; Tadwalkar et al., 2012) to determine the dispersal mode, seed and fruit size and tree height of the 49

species and used information based on field observations for the species identified to the genus level (21 species). Dispersal modes were categorized as animal-dispersed, wind-dispersed and self-dispersed (dehiscence or gravity) based on Howe and Smallwood (1982). Plant pollination systems have been shown to be conserved at the family level (Waser et al., 1996), therefore the pollination mode of 35 species was derived from family-level pollinator syndromes from Endress (1994) and pollination mode of 35 other species was determined from genus level information from published studies in Asia (Murali and Sukumar, 1994; Momose et al., 1998; Corlett, 2001, 2004; Devy and Davidar, 2003). Pollination mode was broadly categorized into insect-pollinated, wind-pollinated, bird-pollinated and generalist, the latter category when the tree species was pollinated by more than one of these groups. In our list of 70 tree species, we did not record any bat-pollinated species.

2.2. Analytical methods

Rarefaction curves based on number of individuals encountered in the vegetation surveys were plotted to examine species accumulation patterns for the tree species. We used the vegetation data

collected from additional forest plots for the rarefaction analysis, while all other analyses were based on equal area sampled across successional sites and uncut forest sites. To assess dissimilarity in species composition between the successional and uncut forest sites, we plotted the species dissimilarity matrix calculated using the 'vegdist' function of the vegan package using the Jaccard's distance (Jaccard, 1908), calculated as

$$J = 1 - (a/[a + b + c]),$$

where a = number of species in first site,
b = number of species in second site, and
c = number of species common between the sites.

The distance ranges from 0 (complete similarity) to 1 (complete dissimilarity). For the species composition analysis using Jaccard's distance, we excluded vegetation data from the 2 year old sites since only four trees of two species were recorded, but included the regeneration data for the composition analysis of the regeneration. The structural data collected for adult trees (tree density, basal area and average tree diameter) were summarized and represented graphically.

We undertook the constrained ordination technique Canonical Correspondence Analysis (CCA) for a subset of the species for which trait information was available (70 tree species and 40 species recorded as seedlings and saplings). In CCA, linear combinations of species abundance data in the different successional sites and uncut forest were checked for correlation with the species traits matrix data and illustrated graphically. We had four variables in the interval scale (fruit size, seed size, wood density and tree height) and two variables at the nominal scale (dispersal and pollination mode). For the CCA analysis, we grouped the fruit size of tree species into three size categories: small (<0.6 cm), intermediate (0.6–2 cm) and large (>2 cm) and similarly for seed size categories: small (<0.5 cm), intermediate (0.5–1.5 cm) and large (>1.5 cm). Tree height was categorized as short (⩽10 m), medium (11–20 m) and tall (>20 m). Wood density was categorized as low (⩽0.44 g cm^{-3}), intermediate (0.45–0.53 g cm^{-3}) and high (>0.53 g cm^{-3}). We used Henry et al. (2010) as a reference to classify wood density, in which pioneer species had low wood density (ranging from 0.25 to 0.48 g cm^{-3}), and shade-tolerant trees had a higher wood density (>0.53 g cm^{-3}). We used the R statistical software for all our analyses (R Development Core Team, 2015).

3. Results

3.1. Diversity of communities based on adult trees

Overall, we recorded 112 tree species; we identified 70 tree species, while the remaining 42 tree species were recorded as separate tree species based on local *Adi* names. The tree species richness in the 2, 12, 25, 50-year old sites and uncut forest was 2, 24, 35, 53 and 68, respectively. The rarefaction curves indicate that the tree species richness curves in the 12 and 25 year old site were reaching their plateau, whereas richness was still increasing with sampling effort in the 50 year old site and uncut forest, with maximum number of species encountered from uncut forest (Fig. 2). The rarefied tree species richness for 300 individuals in the 12, 25, 50-year old sites and uncut forest was (mean [± S.E]) 22.68 (±0.99), 21.65 (±2.26), 50.28 (±1.49) and 62.24 (±2.05), respectively.

The two replicates of uncut forest sites, the 50-year old, 25-year old and the 12-year old sites were most similar to each other in terms of tree species composition (Fig. 3). The early successional sites were most similar to each other and the Jaccard's distance between the two replicate sites of different ages generally increased (indicated by higher values on the y-axis), indicating decreasing
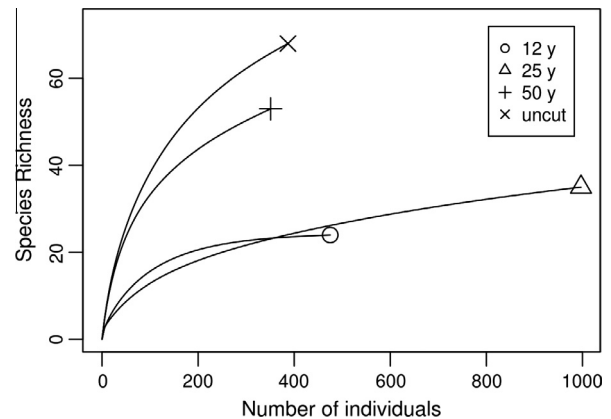

Fig. 2. Rarefaction curves of species accumulation of trees in the 2-year, 12-year, 25-year and 50-year old successional sites formed following shifting cultivation.
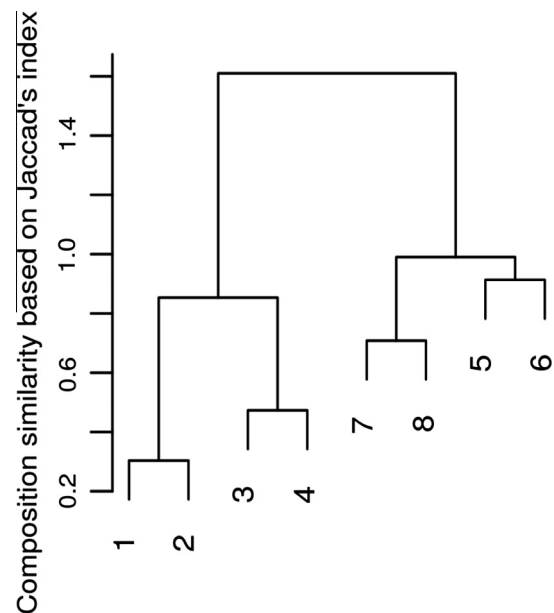

Fig. 3. Dendrogram based on similarities in composition of tree species in the different-aged successional sites and in uncut forest using Jaccard's distance (value ranges from 0 [complete similarity] to 1 [complete dissimilarity]). 1 and 2 represent 12-year old successional sites formed following shifting cultivation, 3 and 4 represent the 25-year old sites, 5 and 6 represent the 50-year old sites and 7 and 8 represent the uncut forest sites.

similarity in species composition in sites with age. Further, the older sites, the 50-year and 25-year old sites, were more similar to each other than the early successional sites, which were more similar to each other. The 2-year old site had four relatively small trees of *Eurya acuminata* and *Michelia* sp., which were likely remnant trees from the previous cultivation phase. In the 12-year old site, *Saurauia nepalensis* and *E. acuminata* were also the most abundant tree species (68% and 11% of all trees, respectively) and in the 25-year old site, *S. nepalensis* and *E. acuminata* comprised about 85% of the trees with approximately equal number of individuals of both species. The abundance of these two species decreased in the 50-year old forest to 24% of individuals. Although *E. acuminata* still remained the most abundant species, tree species of Fagaceae (4) and Lauraceae (6) comprised 35% of tree species in the 50-year old site, along with species belonging to Juglandaceae, Elaeocarpaceae, Meliaceae and Dipterocarpaceae. In the uncut forest, species of the families Fagaceae and Lauraceae were relatively more common (about 60% of individuals and 28% of species).

3.2. Structural parameters of adult trees

The overall basal area of trees in uncut forest was more than twice that in a site that was cultivated fifty years ago (50.1 m^2 ha^{-1} vs. 20.58 m^2 ha^{-1}, averaged across two sites, Fig. 4). The average tree diameter was more than a third higher in uncut forest in comparison with a site regenerating for fifty years (19.6 cm vs. 13.53 cm). Stem density was highest in the 25-year old site (2687 stems ha^{-1}, averaged across two sites) with density lower in the uncut forest site (826 stems ha^{-1}), the 50-year old site (997 stems ha^{-1}) and the 12-year old site (1342 stems ha^{-1}). The basal area and average tree diameter in the 25-year old site were lower than the values in the 12-year old site.

3.3. Species richness and composition of regeneration

We recorded seedlings and saplings of 62 species from the vegetation surveys. Of these, we identified 40 tree species, which were a subset of the 70 tree species identified; the remaining 22 species were recorded as separate species based on local *Adi* names. The number of species recorded as seedlings and saplings in the 2, 12, 25, 50-year old sites and uncut forest sites was 16, 18, 22, 24 and 34, respectively. The number of individuals of seedlings and saplings was highest in the 2-year old site, however the highest number of species recorded was from uncut forest (Fig. 5). The rarefied species richness for 100 individuals in the 2, 12, 25, 50-year old sites and uncut forest was (mean [± S.E]) 7.97 (± 1.56), 15.92 (± 1.47), 16.67 (± 1.54), 24.0 (± 0.0) and 21.45 (± 1.77), respectively. The 2-year old site had several saplings of the small tree/shrub species *Maesa indica* and *Maesa ramentacea* (about 57% of all saplings recorded), followed by regeneration of *S. nepalensis* (24%) and *E. acuminata* (14%) species. More than a third of the regeneration recorded from the 50-year old site comprised of species from the Lauraceae family. The pattern of similarity in species composition for adult tree species held even for regeneration in the successional sites; regeneration in respective successional sites and uncut forest sites was most similar to each other, but there was no clear pattern in terms of the extent of similarity with age of a site (Fig. 6).

3.4. Patterns in functional traits

Of the 70 tree species, 55 were animal-dispersed, nine were self-dispersed and five were wind-dispersed (see Appendix). The dominant mode of pollination was by insects (45 species), followed by wind (14), generalists (9) and birds (2). Almost half of the species were small-seeded (32 species), while fruit sizes were equally distributed across the three size categories in terms of the number of species recorded. Most of the 70 tree species were of medium height (40 species), 18 were tall and 12 were short-statured trees.

In terms of number of species, the occurrence of dispersal by wind and animals remained relatively similar in the 12, 25 and 50-year old sites and uncut forest, while the 2 year old site had only two tree species which were animal-dispersed (Table 1). Pollination by insects was the most common mode in the successional sites as well as in uncut forest (60–70% of species). However, the percentage of wind-pollinated species increased with the age of the site from 9% in the 12-year old site to 25% of species in uncut forest, while in the 2-yr old site, the two tree species were insect-pollinated. The percentage of species with large fruits increased from 19% in the 12-year old site to 39% in uncut forest sites and percentage of species with large seeds increased from 19% to 28% (Table 1). The percentage of tree species with tall tree height and high wood density increased with the age of site and was the highest in uncut forest.
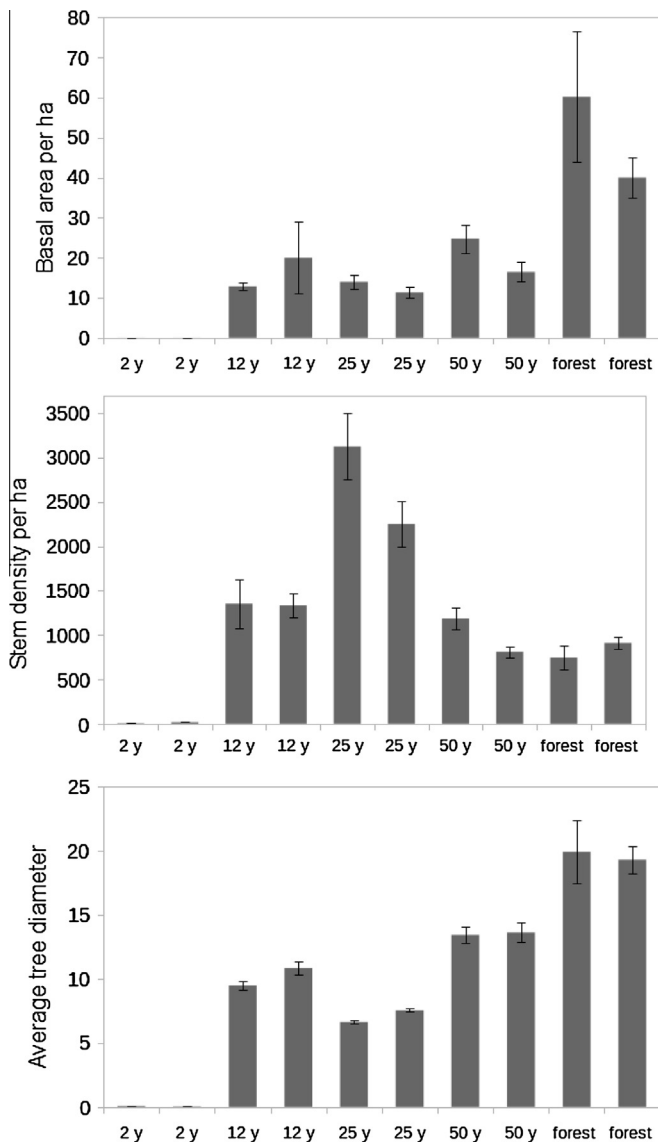

Fig. 4. Basal area (m^2 ha^{-1}), stem density (stems >3 cm diameter at breast height, per ha) and average tree diameter (cm) in two replicates of the 2-year, 12-year, 25-year, 50-year old successional sites and uncut forest sites. Bars represent averaged values with standard error across plots.
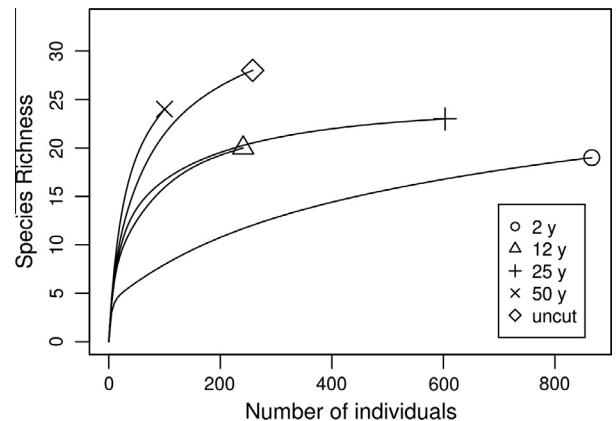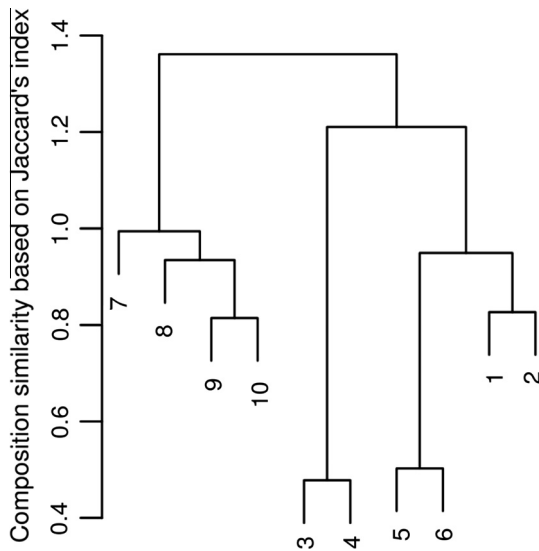

Fig. 5. Rarefaction curves of species accumulation of seedlings and saplings in the 2-year, 12-year, 25-year and 50-year old successional sites formed following shifting cultivation.

Fig. 6. Dendrogram based on similarities in composition of seedlings and saplings of tree species in the different-aged successional sites and uncut forest using Jaccard's distance (value ranges from 0 [complete similarity] to 1 [complete dissimilarity]). 1 and 2 represent 2-year old successional sites formed following shifting cultivation, 3 and 4 represent the 12-year old sites, 5 and 6 represent the 25-year old sites, 7 and 8 represent the 50-year old sites and 9 and 10 represent the uncut forest sites.

More than half of the variation was explained by the CCA axes and the first two axes explained 50% of this variation, with the first axis explaining 40% of the variation (Table 2). CCA1 was positively correlated with the following trait-categories: small seed size (correlation coefficient $r = 0.5$), small fruit size ($r = 0.82$), insect-pollination ($r = 0.62$) and animal-dispersal ($r = 0.85$) and negatively correlated with the following traits: tall tree height ($r = -0.63$), self-dispersal ($r = -0.81$), wind-pollination ($r = -0.64$), high wood

Table 2
Eigen values and correlation coefficients of the first two axes of the Canonical Correspondence Analysis (CCA) undertaken using tree species data in different-aged successional and uncut forest sites.

	CCA1	CCA2
Eigen value	0.49	0.13
Proportion explained	0.40	0.10
Cumulative proportion	0.40	0.50
Correlation coefficients between CCA axes and traits		
Trait categories		
Self-dispersed	−0.81	−0.37
Animal-dispersed	0.85	0.20
Insect-pollinated	0.62	−0.13
Wind-pollinated	−0.64	−0.09
General-pollinated	−0.11	0.29
Small fruit size	0.82	−0.10
Medium fruit size	−0.35	−0.06
Small seed size	0.50	−0.45
Medium seed size	−0.40	−0.10
Tall tree height	−0.63	−0.33
Medium tree height	−0.03	0.60
High wood density	−0.74	−0.10
Medium wood density	0.02	0.40

density ($r = -0.74$) and intermediate fruit size ($r = -0.35$). These two groups of traits were found among distinct sites: the early successional sites had species that were small-fruited, animal-dispersed and insect-pollinated and the uncut forest had species that were wind-pollinated, self-dispersed with tall trees (Fig. 7). Other categories of these traits were not significantly correlated with the CCA1 axis (Table 2). The CCA plot for regeneration also showed grouping of the following traits: (1) small seed size, small fruit size, insect pollination and animal-dispersal, and (2) high wood density, self-dispersal and wind pollination (Fig. 8, Table 3). Seedlings and saplings of species with the first group of traits were recorded from the 2-year old site whereas species with the second group of traits were recorded from the 50-year old site and uncut forest.

Table 1
Summary of percentages of species with different functional trait categories in different-aged successional sites and uncut forest.

Functional traits	2-y fallow (N = 2)	12-y fallow (N = 21)	25-y fallow (N = 31)	50-y fallow (N = 40)	Uncut forest (N = 36)
Dispersal mode					
Self-dispersed	0	9.5	9.7	12.5	19.4
Animal-dispersed	100	76.2	77.4	75	69.4
Wind-dispersed	0	14.3	13	16.1	11.1
Pollination mode					
Insect-pollinated	100	71.4	67.7	60	66.7
Wind-pollinated	0	9.5	16.1	22.5	25
General	0	14.3	13.0	15	8.3
Bird-pollinated	0	14.8	3.2	2.5	0
Seed size					
Small (<0.5 cm)	50	61.9	58.1	47.5	50
Intermediate (0.5–1.5 cm)	0	19	26.0	17.5	22.2
Large (>1.5 cm)	50	19	16.1	35	27.8
Fruit size					
Small (<0.6 cm)	50	47.6	48.4	35	33.3
Intermediate (0.6–2 cm)	50	33.3	22.6	30	27.8
Large (>2 cm)	0	19	29	35	38.9
Tree height					
Small (⩽10 m)	0	24.0	19.3	20	11.11
Intermediate (11–20 m)	100	52.4	51.6	52.5	55.55
Tall (>20 m)	0	24.0	29.0	27.5	33.33
Wood density					
Low (0.44 g cm^{-3})	50	38.09	35.48	32.5	30.55
Intermediate (0.45–0.53 g cm^{-3})	50	33.33	25.8	27.5	25
High (>0.53 g cm^{-3})	0	28.57	38.71	40	44.4
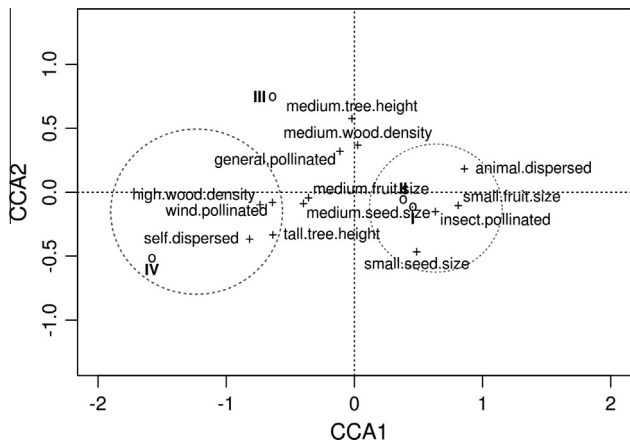
Fig. 7. The Canonical Correlation Analysis plot for tree species from the 12-year, 25-year and 50-year old successional sites (I, II, III, respectively) formed following shifting cultivation and uncut forest sites (IV). Dotted circles indicates clustering of two groups of functional traits: (1) Small seed size, animal-dispersal and insect-pollination, and (2) tall tree height, wind-pollination and self-dispersal. The categories for the traits are as follows: wood density (gm cm^{-3}): low ⩽0.44, intermediate 0.45 to ⩽0.53 and high >0.53, tree height: short ⩽10 m; medium 11–20 m and tall >20 m, fruit size: small ⩽0.6 cm; medium 0.6–2 cm and large >2 cm, seed size: small ⩽0.5 cm, intermediate >0.5 & ⩽1.5 cm, large >1.5 cm, dispersal mode: animal-dispersed, wind-dispersed and self-dispersed (dehiscence or gravity), pollination mode: insect-pollinated, wind-pollinated, bird-pollinated and generalist, the latter category when the tree species was pollinated by more than one of these groups.
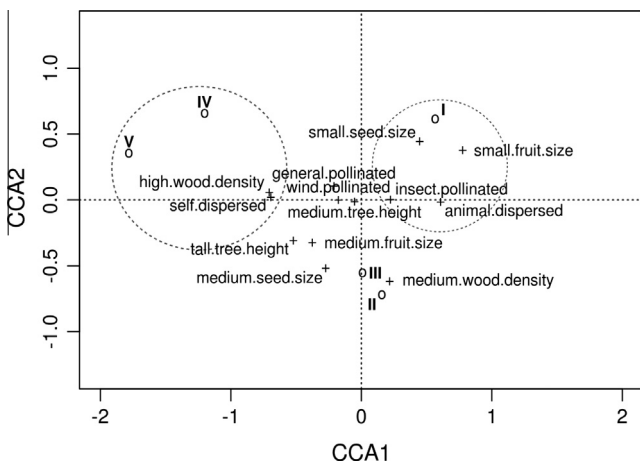
Fig. 8. The Canonical Correlation Analysis plot for seedlings and saplings from the 2-year, 12-year, 25-year and 50-year old successional sites (I, II, II, IV respectively) formed following shifting cultivation and uncut forest sites (V). Dotted circles indicate clustering of two groups of functional traits: (1) Small seed size, small fruit size, animal dispersal and insect pollination, and (2) high wood density, wind pollination and self-dispersal. The categories for the traits are as follows: wood density (gm cm^{-3}): low ⩽0.44, intermediate 0.45 to ⩽0.53 and high >0.53, tree height: short ⩽10 m; medium 11–20 and tall >20 m, fruit size: small ⩽0.6 cm; medium 0.6–2 cm and large >2 cm, seed size: small ⩽0.5 cm, intermediate >0.5 & ⩽1.5, large >1.5, dispersal mode: animal-dispersed, wind-dispersed and self-dispersed (dehiscence or gravity), pollination mode: insect-pollinated, wind-pollinated, bird-pollinated and generalist, the latter category when the tree species was pollinated by more than one of these groups.

4. Discussion

4.1. Structural parameters

Basal area has been shown to be an important predictor of successional changes (Lohbeck et al., 2012). It recovered to about 40% (of the value in uncut forest) in the 50 year-old sites and average

Table 3
Eigen values and correlation coefficients of the first two axes of the Canonical Correspondence Analysis (CCA) undertaken using regeneration data in different-aged successional and uncut forest sites.

	CCA1	CCA2
Eigen value	0.46	0.36
Proportion explained	0.25	0.19
Cumulative proportion	0.25	0.44
Correlation coefficients between CCA axes and traits		
Trait categories		
Self-dispersed	−0.69	0.02
Animal-dispersed	0.60	−0.02
Insect-pollinated	0.22	0
Wind-pollinated	−0.17	0
General-pollinated	−0.21	0.10
Small fruit size	0.77	0.37
Medium fruit size	−0.37	−0.32
Small seed size	0.44	0.44
Medium seed size	−0.27	−0.51
Tall tree height	−0.52	−0.30
Medium tree height	−0.05	−0.01
High wood density	−0.70	0.06
Medium wood density	0.21	−0.62

tree diameter recovered to about 70% of the value in uncut forest in the 50 year old sites. Basal area has been shown to take longer to recover; Saldarriaga et al. (1988) modeled basal area in successional sites formed following shifting cultivation and estimated that it can take close to 200 years to recover to values in mature forest. The stem density was highest in the intermediate-aged sites (12 and 25-year old sites) since these sites had more individual trees but the average tree diameter increased with age and was highest in the uncut forest. This is consistent with patterns recorded from other studies (e.g. Saldarriaga et al., 1988; Van Gemerden et al., 2003; Ruiz et al., 2005). However, the average basal area and tree diameter in the 25-year old site were lower than the site recovering for 12 years. A possible explanation for this is that sites not re-cultivated beyond a period of about a decade are often sites that were relatively unproductive in their previous cultivation phase; therefore the forest recovery in such sites may also be relatively slower.

4.2. Species richness and composition

Tree species richness in the successional sites increased relatively rapidly; over 50% and 80% of the species richness in uncut forest was recorded in the 25-year and 50-year old sites respectively. Species richness in other successional sites recovered to more than 85% within 50 years in comparison with adjoining mature forest (Saldarriaga et al., 1988; Van Gemerden et al., 2003; N'Dja et al., 2008), whereas richness was lower than that in a mature forest even after 100 years of succession following shifting cultivation in Mizoram state in north-east India (Raman et al., 1998). In the regeneration recorded in the 2-year old successional site, species richness was already half that in uncut forest. The 2-year old early successional sites were dominated by seedlings and saplings of the small tree/shrub species *M. indica* and *M. ramentacea*. Fruits of these species are small and widely dispersed by smaller frugivorous birds and it is likely that these species form the first stage of succession before the tree species are established. *M. indica* was recorded as a forest-gap adapted early-successional species in southern India (Ganesh and Davidar, 2001; Chetana and Ganesh, 2012). Seedlings and saplings of other species such as *S. nepalensis* and *E. acuminata*, were also relatively more common in the 2-year old site. Trees of these two species, which are small-seeded, bird-dispersed and insect-pollinated, dominated the two next successional stages comprising sites that were 12 years and 25 years old. The abundance of these species

reduced to very few individuals in the 50-year old site and they were not recorded from uncut forest.

E. acuminata was also recorded as a dominant pioneer species in 20–29 year old sites abandoned following poppy cultivation (Schmidt-Vogt, 2001; Fukushima et al., 2008) and was relatively abundant in three-year old successional sites (Wangpakapattanawong et al., 2010) in northern Thailand. Other species of this genus (*Eurya nitida* and *Eurya trichocarpa*) have been recorded as dominant in the early fallow stage (7–10 years) in other sites (Ding and Zang, 2005; Van Do et al., 2010). It has been suggested that *E. acuminata* facilitates biomass recovery during succession since it produces small berries that are widely dispersed by birds, and may also regenerate even after agricultural operations such as uprooting, hoeing and burning (Fukushima et al., 2008). The other dominant tree species in 12 and 25-yr old sites was *S. nepalensis* which is also a small-sized tree with small fruits dispersed by birds and common in open and degraded areas.

Although in terms of species, most species were insect-pollinated in all sites, when abundance was accounted for, the uncut forest was dominated by wind-pollinated tree species. The uncut forest and the 50-year old site had relatively more individuals of the Fagaceae family (*Castanopsis* sp. and *Quercus* sp.), which are of tall height, self-dispersed and wind-pollinated (27% and 17%, respectively). Species of the Fagaceae family had the largest biomass in uncultivated forest stands in northern Thailand (Fukushima et al., 2008) and *Castanopsis fargesii* was a climax evergreen forest species in Zhejian Province, China (Yan et al., 2007). *Castanopsis indica* was also one of the dominant species in the forest adjoining a shifting cultivation landscape in Meghalaya State in north-east India (Singh and Ramakrishnan, 1982).

Wind pollination is known to be rare in tropical forests and is more common in temperate forests (Bawa, 1990). The contrasting pattern that we found of wind-pollinated species as the climax species in uncut forest is likely due to our study site being located in a sub-tropical relatively higher elevation forest in the Himalaya, where members of Fagaceae are often the dominant family. Further, Kaul (1986) suggested that trees of the Fagaceae family, particularly of the *Quercus* genus are wind-pollinated due to low insect pollination activity in seasonal climates which is the case in our sub-tropical study site.

In terms of dispersal mode, only 19% and 11% of species in the mature forest were self- and wind-dispersed respectively, and 70% of species were of Lauraceae, which are only dispersed by birds (see Appendix 1). However, in terms of abundance, the older site and the uncut forest were dominated by Fagaceae species. These bear medium to large-sized hard seeds (with no fruit pulp) that are self-dispersed (gravity) and maybe secondarily dispersed by terrestrial rodents. In this region, the early site is clearly dominated only by small-fruited, insect-pollinated, and animal-dispersed tree species (mainly small frugivorous birds). Even though later successional sites continue to have a high proportion of insect-pollinated and animal-dispersed tree species, as succession progresses they tend to become dominated by mature forest species with contrasting functional traits. These differences in trait patterns with succession between our site and the Neotropics possibly are partly due to elevational differences in tree community composition in mature forests. Many of the Neotropical study sites are located in lower elevation forests (e.g. Saldarriaga et al., 1988; Tabarelli and Peres, 2002) while subtropical forests across the Himalaya are dominated by wind-pollinated and self-dispersed tree species. The richness and diversity of avian and mammalian frugivores and seed dispersers in temperate forests and subtropical forests is lower than in low-elevation tropical forests (Howe and Smallwood, 1982). More tree species rely on self-dispersal or secondary dispersal by scatter-hoarding rodents and/or seed-eating birds in subtropical forests.

Although species richness in the 50-year old site had recovered to 80% of the value in uncut forest, the site had only about 40% species in common with those in uncut forest. Schmidt-Vogt (2001) suggested that the species assemblage in a successional site is unlikely to be identical to that in a mature forest, given that mature forest is usually found on hilltops or ridges whereas secondary successional sites selected for cultivation are often located on hillslopes. In this study, however, we chose uncut forest sites that were within the shifting cultivation mosaic and were not topographically different. In addition, forests that are considered mature and undisturbed in a shifting cultivation landscape by many studies may be prone to other disturbances such as selective felling and grazing and may not necessarily be strictly 'mature and undisturbed', which is the case with the present study.

4.3. Functional traits

The CCA analysis indicated two distinct groupings of traits: (1) tall tree height, wind-pollination, self-dispersal and high wood density, and, (2) animal-dispersal, insect-pollination, small seed size and small fruit size. This pattern was mostly consistent with the pattern for regeneration in the different-aged successional sites and uncut forest sites as well. Species with these groups of traits were found in distinct sites: the uncut forest and 50 year old site had species with the first group (about 30% and 10% of all trees recorded from these sites) and the 12 and 25-year old sites had species with the second group (about 87% of all trees recorded from these sites).

In Neotropical forest sites, insect pollination and wind dispersal have been shown to be more common in young secondary forests than old growth forests where animal-dispersal and mammal pollination is more prevalent (Chazdon et al., 2003). Similarly, Dölle et al. (2008) and Tabarelli and Peres (2002) found that tree species with wind dispersal reduced while number of tree species dispersed by animals increased with succession. They also found that the seed weight and seed size of plant species significantly increased with succession. Similar patterns were recorded from studies in Asia. In northern Thailand, primary forest had tree species with heavier wood and larger seeds than species in plantations and sites abandoned following shifting cultivation for 30 years (Asanok et al., 2013). In terms of leaf-related traits, it was found that leaf nutrient concentration and robustness increased with succession in south-east China (Kröber et al., 2012).

In this study, although seed size of species increased with succession, our findings differ in the patterns for other traits. Abiotic pollination and dispersal were more prevalent in older fallows and uncut forest. The tree species recorded from mature uncut forest were largely of the Fagaceae family (about 18% of the species and 27% of the individuals in mature forest). Species of this family which are generally dominant mature forest species in subtropical forest sites in the Himalaya are self-dispersed and wind-pollinated. This indicates that succession patterns in terms of functional traits are site- and elevation-specific.

These results have implications for planning and management of restoration efforts in abandoned fields or fallows where it may be important to consider planting early successional pioneer species first allowing natural successional mechanisms to proceed, and mature species can be introduced in mid- and old successional where they are more likely to establish and survive.

5. Conclusion

Species richness and basal area recovered relatively rapidly in our study area, whereas species composition similarity recovered very slowly and even after five decades was less than 50% similar

to the composition in uncut forest. The analysis of species composition using functional traits was useful in identifying distinct traits that characterize species in different stages of succession. Contrary to the findings of earlier studies from Neotropical sites, wind pollination and self-dispersal were more dominant in late successional sites and uncut forest. Early successional sites had a majority of small-fruited, animal-dispersed and insect-pollinated tree species, which implies that dispersal by small birds, and pollination by insects is important in these sites. Dispersal of tree species in early successional sites by birds is likely facilitated due to the interspersion of disturbed and uncut forests in the shifting cultivation landscape, which suggests that retaining forests in a shifting cultivation landscape is important for forest recovery. A trait-based analysis gave us useful insights in understanding patterns of forest recovery following shifting cultivation and demonstrated the importance of documenting site- and elevation-specific trends in succession.

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2016.01.006.

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